ridge of some sharpness between the places is to create a distinct
shadow, to such an extent that the effect would be inappreciable ; the
same result would be produced by an intervening headland ; this
agrees with the experience of Captain Jackson.*

" Studies in the Morphology of Spore-producing Members.—No. V.
General Comparisons, and Conclusion."   By F. O. Bower,
Sc.D., F.R.S., Regius Professor of Botany in the University of
Glasgow.   Received January 30,—Read February 12, 1903.

(Abstract.)

This concluding Memoir contains a general discussion of the results
acquired in the four previous parts of this series, and of their bearing
on a theory of sterilisation in the sporophyte.   The attempt is made
to build up the comparative morphology of the sporophyte from
below, by the study of its simpler types ; the higher and more
specialised types are left out of account, except for occasional com-
parison.   It is assumed for the purposes of the discussion that alter-
nation of generations in the Archegoniatæ is of the antithetic type,
and that apogamy and apospory are abnormalities, not of primary
origin.

After a brief allusion to facts of sterilisation in the Sporogonia of
Bryophytes, the similar facts are summarised for the Pteridophytes.
It has been found that examples of sterilisation of potentially sporo-
genous cells are common also in vascular plants, while occasionally
cells which are normally sterile may develop spores.   Hence it is
concluded that spore-production in the Archegoniate plants is not in
all cases strictly limited to, or defined by, preordained formative cells,
or cell-groups.   A discussion of the archesporium follows, and though
it is found that in all Pteridophyta the sporogenous tissue is ultimately
referable to the segmentation of a superficial cell, or cells, still in
them, and indeed in vascular plants at large, the segmentations which
lead up to the formation of spore-mother-cells are not comparable in
all cases ; in fact, that there is no general law of segmentation under-
lying the existence of that cell or cells which a last analysis may
mark out as the " archesporium "; nor do these ultimate parent cells
give rise in all cases to cognate products.   Therefore it is concluded
that the general application of a definite term to those ultimate parent
cells which the analysis discloses has no scientific meaning, beyond the
statement of the histiogenic fact.

Further, it is shown that the tapetum is not a morphological constant,

* ' Roy. Soc. Proc.,' 1902.

but varies both in occurrence and origin; that even the individuality of the sporangium is not always maintained. All that remains then as the fundamental conception of the sporangium in vascular plants is the spore-mother-cell, or cells, and the tissue which covers them in, for such cells are always produced internally. The definition of the sporangium may then be given thus: " *Wherever we find in vascular plants a single spore-mother-cell, or connected group of them, or their products, this with its protective tissues constitutes the essential of an individual sporangium.*" From the point of view of a theory of sterilisation such sporangia may, at least in the simplest cases, be regarded as islands of fertile tissue which have retained their spore-producing character, while the surrounding tissues have been diverted to other uses. It will be seen later how far this view will have to be modified in the more complex cases.

In a second section of the Memoir the variations in number of sporangia in vascular plants are discussed; the methods of variation may be tabulated as follows, under the heads of progressive increase and decrease :—

I.—*Increase in Number of Sporangia.*

(*a*.) By septation, with or without rounding off of the individual sporangia.

(*b*.) By formation of new sporangia, or of new spore-bearing organs, which may be in addition to, or interpolated between those typically present.

(*c*.) By continued apical, or intercalary growth of the parts bearing the sporangia.

(*d*.) By branching of the parts bearing the sporangia.

(*e*.) Indirectly, by branchings in the non-sporangial region resulting in an increased number of sporangial shoots; this is closely related to (*c*) and (*d*).

II.—*Decrease in Number of Sporangia.*

(*f*.) By fusion of sporangia originally separate.

(*g*.) By abortion, partial or complete, of sporangia.

(*h*.) By reduction or arrest of apical or intercalary growth in parts bearing sporangia.

(*i*.) By fusion of parts which bear the sporangia or arrest of their branchings.

(*j*.) Indirectly, by suppression of branchings in the non-sporangial region, resulting in decreased number of sporangial shoots; this is closely related to (*h*) and (*i*).

We are justified in assuming that (subject to the possibility of other factors having been operative of which we are yet unaware)

the condition of any polysporangiate sporophyte as we see it is the resultant of modifications such as these, operative during its descent.

The problem will, therefore, be in each case to assign its proper place in the history to any or each of these factors.

It is pointed out that in homosporous types, which are certainly the more primitive, the larger the number of spores the better the chance of survival, and hence, other things being equal, increasing numbers of spores and of sporangia may be anticipated; but in the heterosporous types reduction in number both of spores and of sporangia is frequent. The former will accordingly illustrate more faithfully than the heterosporous forms the story of the increase of complexity of spore-producing parts. The general method put in practice here is to regard homosporous forms as in the upgrade of their evolution, as regards their spore-producing organs, unless there is clear evidence to the contrary. The *onus probandi* lies rather with those who assume reduction to have taken place in them.

A summary of evidence of variation in number of sporangia by any of these methods is then given for the Lycopodineæ, Psilotaceæ, Sphenophylleæ, Ophioglossaceæ, Equisetineæ, and Filicineæ; followed in each case by a theoretical discussion of the bearing of that evidence on the morphology of the spore-producing members. The general result is that all of them, including even the dorsiventral and megaphyllous types, are referable to modifications of a radial strobiloid type; progressive elaboration of spore-producing parts, followed by progressive sterilisation, and especially by abortion of sporangia in them, of which there is frequent evidence, together with the acquirement of a dorsiventral structure, may be held to account for the origin of even the most complex forms. But the vegetative organs once formed may also undergo elaboration, and differentiation *pari passu* with the spore-producing organs, a point which has greatly complicated the problem, especially in the higher forms; all roots are probably of secondary origin; facts of interpolation of additional sporangia, especially in Ferns, and of apogamy and apospory, are also disturbing influences, which have probably been of relatively recent acquisition.

A comparison is drawn as regards position, physiological and evolutionary, in the sporophyte between the fertile zone in certain Bryophytes and the fertile region of certain simple Pteridophytes, *e.g.*, the Lycopods; though no community of descent is assumed, the relation of the reproductive to the vegetative regions is the same. In the Bryophytes that region is regarded as a residuum from progressive sterilisation; it is suggested that the same is the case for a strobiloid Pteridophyte, such as *Lycopodium*. The theory of the strobilus, based on this comparison, is that similiar causes would lead to

the decentralisation of the fertile tissue in the primitive Pteridophytes
as in the Bryophytes, and result in the formation of a central sterile
tract, with an archesporium at its periphery; that such an archesporium,
instead of remaining a concrete layer as it is in the larger Musci,
became discrete in the Lycopods; that the fertile cell-groups formed
the centres of projecting sporangia, and that they were associated
regularly with outgrowths, perhaps of correlative vegetative origin,
which are the sporophylls.

Whether or not this hypothesis of the origin of a Lycopod strobilus
approaches the actual truth, comparison points out the genus *Lyco-
podium* as a primitive one, characterised by more definite numerical
and topographical relation of the sporangia to the sporophylls than in
any other type of Pteridophyta.

Then follows, as a consequence of comparison, the enunciation of a
theory of the sporangiophore, a word which is here used in an ex-
tended sense to include not only the spore-producing organs of
Psilotaceæ, Sphenophylleæ, Ophioglossaceæ, Equisetaceæ, but also the
sori of Ferns. The view is upheld that all these are simply placental
growths, and not the result of "metamorphosis" of any parts or
appendages of prior existence; that the vascular supply, which is not
always present, is not an essential feature; that they are seated at
points where in the ancestry spore-production has been proceeding on
an advancing scale; hence they do not occupy any fixed and definite
position. It seems probable that at least a plurality of sporangia
existed on primitive sporangiophores, and that where only one exists
that condition has been the result of reduction.

The above theories are then applied to the several types of Pterido-
phyta. The Lycopods, Psilotaceæ, Sphenophylleæ, and Ophioglossaceæ
may be arranged as illustrating the increased complexity of the spore-
producing parts, and of the subtending sporophylls; the factors of
the advance from the simple sporangium to the more complex spor-
angiophore are, septation, upgrowth of the placenta with vascular
supply into it, and branching, with apical growth also in the Ophio-
glossaceæ. But even in the most complex forms the sporangiophore
may be regarded as a placental growth, and not the result of transfor-
mation of any other member.

In the case of *Helminthostachys* the marginal sporangiophores are
regarded as amplifications from the sunken sporangia of the *Ophio-
glossum* type; in *Equisetum* they are regarded as being directly seated
on the axis, and having originated there by a similar progression:
they would thus be non-foliar. It is pointed out that though a foliar
theory would be possible for *Equisetum* itself, it is not applicable to
the facts known for the fossil Calamarieæ, which are so naturally
related to it. Thus the strobilus of the Equisetineæ is of a rather
different type from that of the Lycopods, Psilotaceæ, or even the

Ophioglossaceæ, in all of which there is a constant relation of the spore-producing parts to the leaves ; in the Equisetineæ no such constant relation exists ; the leaves and sporangiophores may be in juxtaposition, as in *Calamostachys*, without exactly matching numerically ; or the sporangiophores may occur in larger numbers and in several ranks, between successive leaf-sheaths, as in *Phyllotheca* and *Bornia* ; or without any leaves at all, as in *Equisetum*. Thus, on a non-phyllome theory the latter may be held to be only an extreme case of what is seen in certain fossils.

The Ferns, notwithstanding their apparent divergence of character from other Pteridophytes, may also be regarded as strobiloid forms, with greatly enlarged leaves ; the primitive sori of the Simplices resemble the sporangiophores of other Pteridophytes ; the more complicated soral conditions of the Gradatæ and Mixtæ were probably derivative from these, the chief difference being due to the interpolation of new sporangia, an innovation which is in accordance with biological probability, as well as with the palæontological record.

The effect of the results thus obtained on the systematic grouping of the Pteridophytes is then discussed ; it is pointed out that the Lycopods, Psilotaceæ, Sphenophylleæ, Ophioglossaceæ, and Filices illustrate lines of elaboration of a radial strobiloid type, with increasing size of the leaf. The division of Pteridophyta by Jeffrey, on anatomical characters, into small-leaved Lycopsida, and large-leaved Pteropsida is quoted ; but it is concluded that the anatomical distinction of Jeffrey does not define phylogenetically distinct races, but is rather a register of such leaf-development as differentiated them from some common source. It is contended that the Ophioglossaceæ and Filices, which constitute Jeffrey's Pteropsida, are not necessarily akin on the ground of their large leaves, and consequent phyllosiphonic structure ; but that they probably acquired the megaphyllous character along distinct lines. The opinion of Celakovsky is still held, " that the Lycopods are probably of living plants, the nearest prototypes of the Ophioglossaceæ." The more recent investigations of Jeffrey, and of Lang, have shown, however, that in the gametophyte of the Ophioglossaceæ, there is an assemblage of " Filicinean " characters, which differ from those of *Lycopodium* itself. But Celakovsky's comparison is *with the Lycopods, not with the genus Lycopodium* ; so far as the facts go, increasing " Filicinean " characters of the gametophyte follow in rough proportion to the larger size of the leaf ; thus from *Isoetes* we learn that a combination of cross characters is found in a megaphyllous Lycopod type. What we find in the Ophioglossaceæ is that in conjunction with their more pronounced megaphyllous form, still retaining, however, the Lycopodinous type of the sporophyte, they show more pronounced " Filicinean " characters of the gametophyte, and of the sexual organs. It is unfortunate that the facts relating to

the gametophyte of the Psilotaceæ and Sphenophylleæ are not avail-
able in this comparison.

It is not obvious what the meaning is of this parallelism between
leaf-size and characters of the sexual organs; a further difficulty
in its interpretation lies in the fact that for the Equiseta the parallel-
ism does not hold; there " Filicinean " characters of the gametophyte
accompany entirely non-Filicinean characters of the sporophyte, the
latter showing nearer analogy to the Lycopods than to the Ferns.
Such cross characters are difficult to harmonise with any phylogenetic
theory ; on account of them, the Equisetineæ are placed in an isolated
position, and in the same way, though with less pressing grounds, a
separate position should be accorded to those types which lie between
the extremes of Lycopods and Ferns, in proportion as the characters
are more or less pronounced.

On this basis the Isoetaceæ would probably best take their place as
a sub-series of the Lycopodiales, Ligulatæ ; the Psilotaceæ and Spheno-
phylleæ would constitute a series of Sphenophyllales, separate from,
but related to, the Lycopodiales.   The Ophioglossaceæ would form an
independent series of Ophioglossales, more aloof than the latter from
the Lycopodiales, but not included in the Filicales.   The actual con-
nection of these series by descent must remain open ; it is quite
possible that some or all of them may have originated along distinct
lines from a general primitive group, which may be provisionally
designated the Protopteridophyta ; these were probably small-leaved
strobiloid forms, with radial type of construction, and with the
sporangia disposed on some simple plan.   The grouping arrived at in
these Memoirs may be tabulated as follows :—

PTERIDOPHYTA.

I. LYCOPODIALES.

(*a*) Eligulatæ.
  Lycopodiaceæ.

(*b*) Ligulatæ.
  Selaginellaceæ.
  Lepidodendraceæ
  Sigillariaceæ.
  Isoetaceæ.

II. SPHENOPHYLLALES.

  Psilotaceæ.
  Sphenophyllaceæ.

III. OPHIOGLOSSALES.

  Ophioglossaceæ.

IV. FILICALES.

(*a*) Simplices.

Marattiaceæ.
Osmundaceæ.
Schizaeaceæ.
Gleicheniaceæ.
Matonineæ.

(*b*) Gradatæ.

Loxsomaceæ.
Hymenophyllaceæ.
Cyatheaceæ.
Dicksonieæ.
Dennstaedtiinæ.
Hydropterideæ (?).

(*e*) Mixtæ.

Davallieæ.
Lindsayeæ.
Pterideæ, and other Polypodiaceæ.

V. EQUISETALES.

Equisetaceæ.
Calamarieæ.

"On the Negative Variation in the Nerves of Warm-blooded
Animals." By N. H. ALCOCK, M.D.   Communicated by
A. D. WALLER, M.D., F.R S.   Received January 17,—Read
February 12, 1903.

(From the Physiological Laboratory, University of London, S.W.)

Introduction.

The negative variation in the nerves of warm-blooded animals has
already been the subject of several researches.* While the nerves are
still in connection with the tissues it has been the experience of most
observers that there is no difficulty in examining the negative variation,

* Valentin, 'Pflüger's Archiv,' vol. 1, p. 423; Fredericq, 'Du Bois Archiv,'
1880, p. 70; Hermann, 'Physiologie,' vol. 2, p. 120; Gotch and Horsley, 'Phil.
Trans.,' "Croonian Lecture," 1891, p. 267; Macdonald and W. Reid, 'J. Physiol.,'
vol. 23, p. 100; Waller, 'Animal Electricity,' London, 1897; Boruttau, (*a*)
'Centralbl. f. Physiologie,' vol. 12, p. 317, 1898, (*b*) 'Pflüger's Archiv,' vol. 84,
p. 309, 1901.